



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE AMERICAN NATURALIST

VOL. XLV

January, 1911

No. 529

ORGANIC RESPONSE¹

D. T. MACDOUGAL, PH.D., LL.D.

DESERT LABORATORY, TUCSON, ARIZ.

AT no time in the history of natural science has such a large share of thought and research energy been directed to the solution of evolutionary problems as at present. Methods of work, plans for experimentation and modes of interpretation have recently undergone such rapid development and improvement that our potentiality for solving questions in heredity and origination is vastly greater than even at such recent date as the beginning of this new century. With increased facility in attack has also come wider vision and altered viewpoints with regard to almost all phases of biology.

Biological thought once quickened and broadened by evolutionary ideas was by this same means led to become entangled in a maze of illusive assumptions as to purpose and plan in organisms from which it is being but slowly freed, to view functions as inevitable reactions, however complex they may be. The variables included in the equations of protoplasmic action are numerous and large, but they do not exceed the undefined principles of osmotic action, surface tension and unknown phases of association and dissociation that are concerned in the interplay of substances in the cell, and upon which

¹ Presidential address, Society of American Naturalists, Ithaca, New York, December 29, 1910.

depend the chemico-physical relations of tissue components and structures of all kinds. If physiology escapes the soporific and deadening influence of the vitalistic conceptions, now appearing in some profusion, it may in turn furnish the secure means for a long and rapid advance in genetics, and it may be assumed with some certainty that the chief superstructures of evolutionary science will be those securely raised upon a foundation of physiologically tested facts.

In taking this direction, natural history is not alone; the briefest comprehensive view of the physical sciences will show that here also the chief advance lies along the way of the study of energetics, and that the fundamental problems are those lying about the mode and means of transformations of energy.

Recent events in the field of evolution comprehend a number of movements and accomplishments of extraordinary interest. The rediscovery of the facts of alternative inheritance, the formulation of the concepts of equivalent, balanced, paired or differential characters, the results of statistical studies of variability, the analyses of species of various constitution by pedigree cultures, in which the value of fertilization from various sources is carefully measured, the distinction of the biotype or genotype as a hereditary entity, the possibilities in the action of pure lines within a specific group, the cytological contributions of fact and forecast upon the physical aspects of heredity, and lastly the presentation of the facts and allowable generalizations identified with the mutation theory, comprise a series of advances, of accretions to knowledge, furnish a broadened foundation for biological science, and disclose additional possibilities in all lines of experimental research with living things, besides opening up new realms for speculative thought, and stimulating the scientific imagination to renewed fruitfulness.

Biological literature has also been recently enriched by a series of formal papers commemorative of the life and work of Charles Darwin, by more than fourscore workers

representing the laboratories and national cultures of the world. This group of addresses and essays, fortunately written chiefly within four languages, taken collectively, constitutes a critical and evaluatory discussion of the mass of fact and galaxy of theory concerning organic evolution, and furnishes the most complete and thorough appraisal ever made of any subject in modern biology.

The moment, therefore, is one of consciousness of achievement, of realization of increased powers of penetration, and charged with desire for the exploitation of the unknown, and is vibrant with the inspiration coming from such a rapid march of events. With this quickening in activity, the outcries of acrid controversies no longer monopolize our attention, but it must not be supposed that differences of opinion have vanished from among us. The agreement as to the value of methods of experimentation and calibration is a most gratifying fact, but the harmonies of opinion as to interpretation of results have not yet come to a monotone.

On the contrary, the pressure of new and undisciplined evidence has awakened a freshened chorus of voices crying the virtues of special interests and extolling the sufficiency of theories dignified by age and more or less weighty with authority. Those busy with vitalism of various patterns have spun a moiety of their favorite fabric to mend the breaks in the fragile web made by the impact of new facts. Isolation and the mechanism of geographical distribution have again been elaborated to account for all differentiation and what their exponents are pleased to term speciation. The anticipatory formation of structures in a rudimentary condition with a long prefunctional progress, guided by the morphological possibilities and actuated by internal impulses, has again been offered to us, fortified by paleontological fact and clever logic, in such manner as to avoid most of the serious objections to orthogenesis except those of physiological morphology.

Natural selection with diverse meanings and manifold implications has been made to explain development, differentiation and general evolutionary progress. The tumult is greatest at the present time, however, about the idea of mutation. Standing to one side, the biologist hears a medley of assertions "that mutations have long been known," "do not exist," "were discovered by Darwin," "are always an evidence of hybridization," "result in the formation of nothing but elementary species," "give only weakened derivatives that are quickly swamped by parental forms," "are encountered only among cultivated plants," "the mutation theory is based upon the conception of unit characters," "constitutes the only adequate means of accounting for the enormous number of living forms and myriad characters of living things," "unit characters are unreal, have never been seen, do not exist and are incapable of demonstration." "The difference between mutation and variation is one of amplitude only," and lastly mutation signally "refutes Darwinism," and "swings us back in harmony with the theologian's arguments for special creation."

The absurdity of the many injudicial assertions by the partisans concerned need not blind us to the stubborn fact that saltatory changes do occur in hereditary pure lines in a large number of forms in both plants and animals. Observations and experiments have established beyond doubt that mutation is one way by which organisms bearing new combinations of qualities may arise, although it is probable that its importance as a general procedure varies in different groups of organisms and certain that many shades of opinion as to its exact part in the evolution of living things will always be held.

Our appraisalment of the value of all the protheses cited may also be amended from time to time with viewpoints altered by the advance of knowledge. The situation with regard to one hypothesis is far more serious, however. This is the theory which predicates direct adaptational adjustment of the organism, quickly or

slowly as the case may be, to environic factors, and the inheritance of the somatic alterations constituting such variations. The various corollaries of this theory have the force of a certain obviousness, its assumptions have been of ready service to the systematist and biogeographer, and its conclusions have long been tolerated in the absence of decisive tests which are not to be easily made or readily carried out. The time has now arrived, however, when the claimants for Neo-Lamarckianism and all of its conclusions must show cause for its further consideration, or else allow it to drop from the position of being seriously taken as a method of evolutionary advance.

It is unanimously agreed that organisms, plants as well as animals, change individually in aspect, in form and structure of organs, in functionation and habit as they encounter swamps, saline areas, gravelly uplands or slopes, climatic differences identifiable with latitude or elevation, and other physical and biological factors. It is assumed that these somatic alterations are accommodative and adaptive, making the organism more suitable for the conditions which produce the changes. Such an assumption is an over-reaching one. Any analysis of the changes which an organism undergoes after transportation to a new habitat will disclose one or a few alterations which might be of advantage in dealing with the newly encountered conditions, but with these are many others, direct, necessitous, atrophic, or hypertrophic as to organs which have no relation whatever to usefulness or fitness. Further, a critical examination fails to disclose any theoretical considerations or any actual facts which would connect inevitably the somatic response with the nature of the excitation, outside of the specialized tropisms in which specific reactions are displayed. Even in these the adjustment is of such nature that a mechanism specially perceptive to contact, for example, may react to changes in temperature, as illustrated by the action of tendrils, and many similar cases might be cited. It is evident that the soma of a plant or animal is not to be

considered as capable of adaptive alterations to every new agency which may cause changes in its form, structure or functionation.

Next we come to the very crux of the whole matter: do the unusual forms or activities of organs resulting from environic causes act in any manner upon the germ-plasm connected with such altered bodies? If we are to consider the activities of the organism or of the cell to depend mainly upon its chemical structure and constituency and such a generalization seems unavoidable, then we have means by which the soma might cause its properties to be reflected from the germ-plasm in a succeeding generation, since the chemical mechanism of the soma and germ-plasm must be of the most intimate nature. That some such connection does actually exist is strongly suggested by the behavior of a great number of organisms which have been seen to carry marked environic effects to the second or even third generations; if the interrogation be made as to why the induced qualities are carried no further it may be said that the reply may be suggested by the results of long-continued action of the exciting agency, such as has been used by Woltereck with *Daphnia*.

If a general view be taken of the available information of interest in this connection, three classes of facts will be discerned. One group is comprised in the mass of information obtained by the operations of the horticulturist, the agriculturist and the breeder as to the behavior of crops, plants and domestic animals, when transferred from one habitat to another. The greater part of such data is the result of observations which do not comply with the ordinary requirements in the avoidance of error so that strict comparisons as to the behavior of organisms under conditions of various habitats are impossible. A consideration of the literature yields many suggestions for experimental research and the simple generalization that the direct effects of climatic complexes on the seasonal cycle, and upon color, or struc-

tural features of the individual, may be repeated or carried over two or three generations, in a habitat where the specific causal combinations are lacking. This is the available total of knowledge furnished us by economic operations, and by the introduction operations of botanical gardens and plantations.

In contrast with these the fortunate experience of Zederbauer with *Capsella* has yielded some conclusions of exceptional importance. A genotype of *Capsella Bursa-pastoris* resembling *taraxicafolium* was found on the lower plains of Asia Minor, and displayed the well-known characters of this form, including broad leaves, whitish flowers, and stems 30–40 cm. high. A highway leads from these regions to a plateau at an elevation of 2,000 to 2,400 meters. The conditions of distribution are such as to indicate that the plant has been carried up this thoroughfare by man, and in this elevated habitat it has taken on certain alpine characters, including elongated roots, xerophytic leaves, stems 2–5 cm. high, reddish flowers, with a noticeable increase of the hairiness of the entire plant. That the distributional history has been correctly apprehended seems entirely confirmed by the fact that when seeds are taken from the lowlands the alpine characters enumerated are displayed at once as a direct somatic response. When seeds are taken from plants on the elevated plateau where their ancestors may have been for many years or many centuries (perhaps as long as 2,000 years) and sowed at Vienna and in other cultures carried through four generations the leaves lose their xerophytic form and structure, but the other characters are retained within the limits of variability. The stems show an increase in average length of 1 or 2 cm., the roots change as much, but the reproductive branches and floral organs retain their alpine characters. The slight modifications undergone by these features were seen to reach a maximum and to decrease in the latest generations cultivated. The structural changes and implied functional accommodations are indubitably direct

somatic responses, there is no escape from the conclusion that the impress of the alpine climate on the soma has been communicated to the germ-plasm directly or indirectly in such manner as to be transmissible, and the suggestion lies near that repeated and continued excitation by climatic factors may have been the essential factor in such fixation.²

Among the most noteworthy investigations of the features of interest in connection with habitat changes are those being made by the anthropologist in which somatic calibrations of immigrating races and linguistic studies of peoples of known origin, geographical movement, and established relationship are being used to great advantage. No more fascinating chapters of scientific literature are to be found than those which delineate the migratory movements, segregation and habitual reactions of Polynesian islanders, of North American Indians, or of Asiatic peoples, yet their value as actual contributions to the phase of biology of interest to this society is hardly recognized. The investigator of problems in anthropology has the advantage of dealing with an animal whose psychology, history, traditions and records are readily intelligible to him, so that a much wider range of facts may be brought within the zone of reliability than when we deal with an organism whose actions, at best, are but imperfectly understood by us.³

A second series of results of great interest and suggestiveness are those which have been obtained in various laboratories as to the individual modifications in cyclical activity, functionation and structure of plants and animals in response to unusual stimuli, or under the influence of unusual intensities of the common environic components. The behavior of organisms in constant illumination, equable and variable temperatures, salinity, alkalinity or acidity of the medium, unusual pressures of at-

²“Versuche ueber Vererbung erworbener Eigenschaften bei *Capsella bursa pastoris*,” *Oester. Bot. Zeitschr.*, Vol. 58: pp. 231-236, 285-288, 1908.

³See Boas, F., “Changes in Bodily Form of Descendants of Immigrants,” The Immigration Committee, Document No. 208, presented to the 61st Congress, 2d Session, Washington, D. C., U. S. A., 1910.

mospheric constituents, to unusual compounds and unaccustomed food-material, make up an important proportion of the sum total of information ordinarily classified as physiology. The morphogenic and accommodative adjustments presented afford by analysis the best conceptions available as to the nature of the physiologic activity of organisms.

The experimental results of Stockard with fish eggs subjected to the action of various chemical substances are of unusual interest in the present connection. The cyclopean embryos of *Fundulus* formed in sea-water containing magnesium salts offer the first known example of the induction of an abnormality in the vertebrates occurring in nature, by specific reagents. Suggestion of a common cause is obvious as it is in the instances in which similar divergences have been secured in the laboratory with plants. As will be pointed out later, such analytical tests constitute a very important part of the procedure in the study of acclimatization results.⁴

In very few cases, however, has the permanency or heritability of the deviations induced been tested, and in most of such tests the agencies employed might have acted upon both soma and germ-plasm, as will be apparent upon an examination of the work of Standfuss, Fischer, Pictet and Houssey. The work of these older experimenters has been reviewed so many times that it will be unnecessary to discuss their results further in the present paper. This was done at the Darwin memorial meeting in 1908, and quite recently by Bourne in his address before Section of Zoology of the British Association for the Advancement of Science, at the Sheffield meeting.⁵

The present opportunity may well be used to make a presentation of the results of the last few years obtained

⁴Stockard, C. R., "The Development of Artificially Produced Fish.—The Cyclopean Embryo," *Jour. Exper. Morphology*, Vol. 7, No. 2, p. 285, 1909.

⁵*Nature*, Vol. 84, p. 378, 1910, September 22, 1910.

by investigations, using a more perfected technique, and having the advantage of a keener insight into the real nature of the problems to be solved.

That the general hypothesis with its corollaries is being subjected to the most critical examination and that the assumptions implied in the conception of inheritance of acquired characters are being put to exact and conclusive tests, is readily apparent when a review is made of recent and current researches in which living material from widely separated groups of animals and plants is being subjected to a variety of nutritive conditions and climatic agencies. Klebs, who has long been concerned with the morphogenic reactions of plants, has determined a series of conditions under which the stages of mycelial development, asexual zoospore and sexual or oospore formations in filamentous fungi may be inhibited or variously interchanged. Much more important reactions were obtained from *Sempervivum*, the live-forever of the garden. In this plant, inflorescences were replaced by single flowers by experimental excitation while it was found the number and arrangement of the floral organs as well as of the stamens and carpels could be altered. Furthermore, the deviations in question were found to be transmissible to the second or third generation in guarded seed-reproductions.⁶

Microorganisms with a short cycle offer peculiarly advantageous material by reason of their simple reproductive processes, and also by the fact that it is possible to control environic factors with exactitude. The voluminous literature of bacteriology shows that much attention has been devoted to the building up of characters by selection, and to the study of the behavior of morphological divergences occurring in special cultures.

The experiments of Buchanan with *Streptococcus lacticus* yields the conclusion that phases of fluctuating variations in the bacteria induced by cultures may not be fixed,

⁶ Alterations in the development and forms of plants as a result of environment, Proc. Roy. Soc. Lond., Vol. 82, No. B. 559, p. 547, 1910.

and are not transmissible, which is in accord with the main body of evidence upon this point. There are, however, a number of records of the appearance of definite qualities or morphological characters in the yeasts, which were transmissible and permanent. These departures were so striking as to be capable of being regarded as mutational, and their origin has been ascribed to the influence of the environment by experimenters of notable skill, such as Beijerinck, Winogradsky, Lepeschkin, Hansen and Barber. It may be recalled in this connection, that environic responses are generally sudden, and that the entire range of departure may be made in a single generation, at most in two or three.⁷

Pringsheim after a comprehensive review of his own work and of other available evidence obtained by a study of accommodations or adaptations of yeasts and bacteria to unusual temperatures, culture media, and poisons, concludes that some of these variations are fixed and transmissible both asexually and by spores, while others are not. It is not easy to analyze contributions upon this subject with reference to the differential action of the exciting agencies upon soma or germ-plasm, neither is it clear as to the action of the selection in the experimentation. It is important, however, to note that the alterations concerned are direct functional responses to the exciting agencies.⁸

The researches of Jennings with paramœcium deals with conditions of morphology and physiology not widely dissimilar from those offered by the bacteria with regard to the present problems, and his work has been carried out with an extensiveness and thoroughness impossible to the worker with more massive and more slowly moving organisms. Cultures were carried through hundreds of generations with no progressive action in fluctuating

⁷ For a brief review of this subject see Buchanan, "Non-inheritance of impressed variations in *Streptococcus lacticus*," *Journal of Infectious Diseases*, Vol. 7, p. 680, 1910.

⁸ Pringsheim, H., "Die Variabilität niederer Organismen," Berlin, 1910.

variability; while the organism as a whole was strongly resistant to all kinds of environic influences, and actual alterations were extremely rare. Most of the supposedly acquired characters disappeared in two or three generations by fission, although one was followed for twenty-two generations. The new character was borne by only one of the pair produced by a division, except in rare instances, and in only one case was there found such modification as to produce a race bearing the odd character in which the feature in question was imperfectly transmitted in series of asexual generations.⁹

The results of Woltereck with *Daphnia* offer something by way of contrast and also serve to illustrate the necessity for continuation of parallel cultures for the purpose of comparison of divergent forms and the normal. The particular group of this crustacean furnishing the experimental material is taken to be very variable, and it was subjected to over-feeding with the immediate result that the variability of the form of the head appeared to be widened, the size of this structure being increased. This disappeared when lots from the culture were restored to normal conditions in the earlier stage of the work. After three or four months of over-feeding, the form of the head came within narrower limits, and fewer aberrants were seen, while lots returned to normal conditions, showed a slower restoration of the original form of the head. Two years after the cultures were begun, it was found that the original head form was not displayed by young restored to normal nutrition conditions, the larger helmet being persistent. It seems fairly certain that a new genotype resulted from the long-continued action of the culture medium.¹⁰

⁹ Jennings, H. S., "Heredity and Variation in the Simplest Organisms," AMER. NAT., Vol. 43, No. 510, June, 1909; and other papers by the same author.

¹⁰ "Weitere experimentelle Untersuchungen ueber Artenveränderung speziell ueber das Wesen quantitativer Artenunterschiede bei Daphniden," Sonderabdruck a. d. Verhandl. d. Deut. Zool. Gesell., 1909.

In the experiments of Sumner mice reared in a warm room were found to differ considerably from those reared in a cold room in the mean length of the tail, foot, and ear, and the differences were transmitted to the next generation. The differences may be reasonably designated as being directly individual and somatic, and as having been transmitted by the germ-plasm, which was not subject to the action of various temperatures in the first instance. The reaction forms have an additional claim upon our attention, since they are the ones which distinguish northern and southern races of many animals. The crucial test of the value of the alterations induced in the mice is the one applicable to all of the experimentation on this subject, a test in which two parallel series of cultures, one under the altered environment and the other under usual conditions, should be kept going continuously for a long number of years, lots being withdrawn from both, from time to time, for long-continued comparative culture in normal habitat and under other conditions. Effects due solely to fluctuating variability may be expected to reach a maximum and minimum within two or three years, leaving the enduring effects standing alone, or in such relief as to be capable of ready calibration.¹¹

Kammerer carried out some tests with salamanders three years ago which have the interest attached to any attempt to interpret geographic or habitat relations. *Salamandra maculosa* is viviparous when it lives high in the mountains and ovo-viparous at lower levels. *S. atra* is an alpine form and the larvae are large with very long gills. When the latter form was kept at unusually high temperatures the larvæ produced resembled those of *S. maculosa* in its lower warmer habitats. *S. maculosa* kept in low temperatures and without water showed a cumulation of effects by which the characters of the

¹¹ Sumner, F. B., "An Experimental Study of Somatic Modifications and their Reappearance in the Offspring," *Archiv. f. Entwicklungsmechanik d. Organismen*, Vol. 30, pt. 2, p. 317, 1910.

young and the reproductive habits resembled those of *S. atra*. The conditions of these experiments are not such as to allow a definite separation of somatic and germinal effects, neither was the permanency of the newly acquired habits tested to such an extent as to determine their hereditary value. That characters and habits may be modified in such manner as to appear in the next generation or two in the absence of exciting conditions is illustrated by hundreds of authentic examples in plants which have long been known.¹²

My own earlier work with relation to this subject consisted chiefly of ovarial treatments in which the main and accessory reproductive elements of seed-plants were subjected to the direct action of solutions of various kinds. New combinations of characters constituting a distinct elementary species or genotype were obtained in one plant, and the divergent type has been found to transmit its qualities in the fullest degree as far as tested, to the fifth generation. Still more marked forms were obtained in a second genus, the divergent progeny being lost in transference to the Desert Laboratory, while marked responses have been obtained in the extensions of these experiments upon species representing widely different morphological types in Arizona. The greater majority of the tests have been made upon plants growing under natural conditions, so that environmental reaction in addition to that of the specific reagents might be excluded. Progenies representing many species, including thousands of individuals, many of which are divergent, are now under observation. Absolute finality of decision with respect to the standing of the new types may be reached but slowly.

Gager produced chromosomic aberrations in the reducing divisions of *Oenothera* by irradiations and such excitation was also followed by the appearance of aberrants in the progeny, the hereditary qualities of which have not

¹² *Arch. f. Entwickel.*, Vol. 30, pp. 7-51, 1907.

been tested. Using similar excitation Morgan induced the appearance of white eyes and of short wings in a pedigree culture of the fly, *Drosophila ampelophila*. Both qualities were sex-limited and mendelized when paired with the red eyes and long wings of the original type. Both however seem to be fully transmissible.¹³

A related phase of the subject is that of the interposition of environic factors in mutations and hybridizations. DeVries has repeatedly called attention to the fact that the composition of hybrid progenies of mutants with each other and with the parental form might be altered by nutritive conditions, and the author has cited the fact that mutations were made by *Oenothera Lamarckiana* in the climate of New York which had never been seen in Amsterdam. Furthermore, in discussing the divergent results of DeVries and myself, obtained by crossing the same forms in Amsterdam and New York, the suggestion was made that "the manner in which the various qualities in the two parents are grouped in the progeny might be capable of a wide range of variation. Many indications lead to the suggestion that the dominance and prevalence, latency and recessivity of any character may be more or less influenced by the conditions attendant upon the hybridization; the operative factors might include individual qualities as well as external conditions."¹⁴

Using abnormal temperatures for excitation, Kammerer induced color changes in *Lacerta* constituting female dimorphism in one species, and male dimorphism in another, and the newly induced characters, like the original ones, behave in a mendelian manner in crosses, although the heredity has not been carried through enough generations to test their permanence.¹⁵

¹³ Morgan, T. H., The method of inheritance of two sex-limited characters in the same animal, Proc. Soc. for Exper. Biol. and Med., Vol. 8, No. 1, p. 17, 1910.

¹⁴ MacDougal, Vail, Shull and Small, "Mutants and Hybrids of the *Oenotheras*," Pub. No. 24, p. 57, Carnegie Inst. of Washington, 1905.

¹⁵ Vererbung erzwungener Farbensänderungen. Arch. f. Entwickl., Vol. 39, Hefte 3 and 4, p. 456, 1910.

Much more striking evidence upon the matter has been recently obtained by Tower in intercrossing *Leptinotarsa decemlineata*, *L. multineata*, *L. oblongata* and other species in their habitats in southern Mexico, and at the desert laboratory. Among other divergences one of the three first generation intermediates characteristic of these cultures was lacking from the Tucson cultures, although two other such forms were included.¹⁶ In a

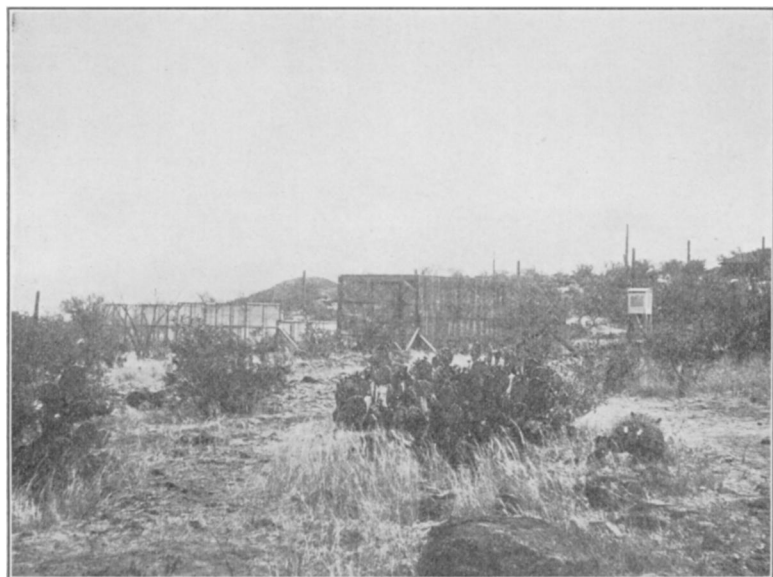


FIG. 1. Acclimatization shelters and beetle cages, Desert Laboratory (2,600 ft.).

comprehensive treatment of the entire subject with especial reference to modifications in dominance Tower says:

The experiments and observations herein given warrant the general statement that conditions external to a cross are important factors in determining the results thereof. This conclusion has been worked out in both normal and hybrid crosses, in crosses between races which have been created selectively, and between forms which arose as sports;

¹⁶ See Report, Department of Botanical Research, Carnegie Institution of Washington, for 1908 and 1909.

and the second series of experiments in synthesis is sufficient warrant for attributing to this factor a considerable importance in evolution.¹⁷

Tennent arranged a series of hybridizations of Echinoderms at Tortugas which yielded data of great interest in connection with the earlier conclusions of Vernon, Doncaster, and Herbst as to the influence of temperature and season changes upon dominance. From the information derived from crosses of Hipponoë and Toxopneustes it is clear that the dominance of the parental characters is dependent upon the alkalinity or the concentration of the OH ions. The products of the trial cross fertilization, however, were not reared to maturity.¹⁸

No phase of the subject under discussion is more readily amenable to experimental investigation, and no results may be expected to bear more directly on the mechanism of inheritance than those in which similar unions give dissimilar progenies under the pressure of unlike environments. It is to be noted that everything of value with regard to the influence of environment upon hybridizations has been secured by the introduction of the geographic or climatic element, that is, the unions leading to divergent results have been made in habitats in which the environic complexes differed not in one, but in many features. Thus the climatic components in southern Mexico reach dissimilar maxima and minima and run unlike courses from those of Arizona.

This method of transplantation of organisms to distant localities furnishing congeries of climatic factors markedly different from those of the habitat in which they were found is one which offers opportunities of the broadest kind, and such exchanges have been made between fresh and salt water, cave and surface, alpine

¹⁷ Tower, W. L., "The Determination of Dominance and the Modification of Behavior in Alternative (Mendelian) Inheritance, by Conditions Surrounding or Incident upon the Germ Cells at Fertilization. (Reprinted from *Biological Bulletin*, Vol. XVIII, No. 6, May, 1910.)

¹⁸ See Report, Director Dept. of Marine Biology, Carnegie Institution of Washington for 1909 and 1910.

summits and lowland plains, high and low latitudes, with results of somewhat limited value until recently. The first of these in which plants were used was made by Nägeli, who carried on observational work on a large number of species in plantations of the botanical garden at Munich, detecting certain obvious alterations which did not appear to offer anything of hereditary value.

The more recent work of Bonnier was directed chiefly toward comparison of the vegetative activity, anatomical modification, and developmental habit of plants exchanged between the mountain and low-land. The care used in attempting to transport soils with the plant was almost wholly without direct application, since the character of the soil is so largely a function of climate that the course of a single season would suffice to change or materially modify any transported soil. Such a precaution might have the sole merit of furnishing the transplanted species with a limited amount of some compound necessary for its growth, but any small amount of soil becomes quickly permeated by solutions from the formations below and contiguous to it. Bonnier's results include much that is suggestive, although no effects were secured which did not disappear within two or three seasons after a plant had been removed from the influence of the exciting agencies or returned to its original habitat.

The first realization of results of importance from cultures widely extended geographically has been obtained in the experiments with *Leptinotarsæ* by Tower, in which various species of these beetles were studied in their habitats in southern Mexico, in open air and glass houses as far north as Chicago, as far east as the Atlantic and as far west as the Desert Laboratory. Facilities for work upon special problems are now being organized at several places and many contributions to the subject may be expected within the next decade.

The plan for work upon the problems of special interest in connection with the Department of Botanical

Research of the Carnegie Institution of Washington, implies the establishment of experimental cultures in localities which furnish distinct types of climate, or which have characteristic complexes of meteoric factors, as indicated by the vegetation indigenous to them. Secondly, these localities have been chosen with regard to their geographical relations so far as possible, in order that the possible and probable fate of migrating species might be studied. The behavior of plants in these localities is

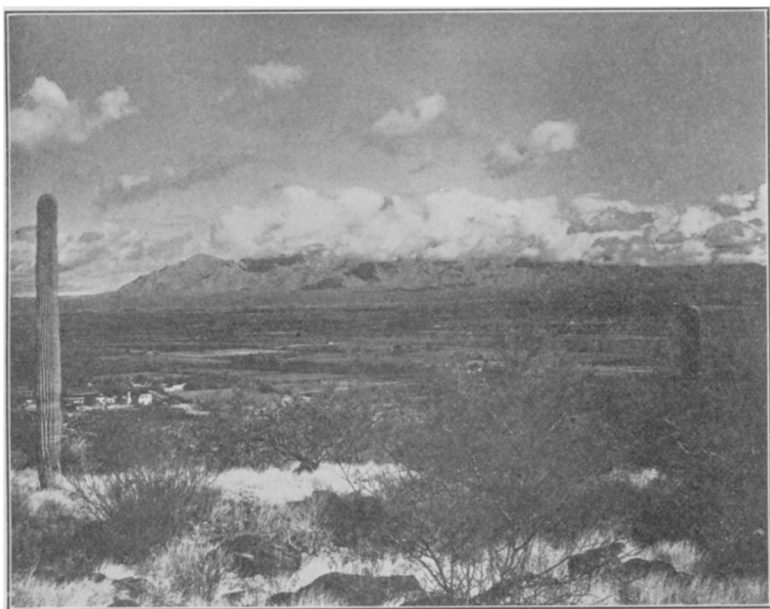


FIG. 2. Santa Catalina mountains as seen from Desert Laboratory. Experimental plantations shown in figures 3 and 4 are located on this range.

recorded as to anatomical alteration and physiological departure. Having detected some such feature of apparent importance, its reappearance in plants from seeds carried to the original habitat and other locations is followed as one line of evaluation. Contemporaneously, the form is taken into the laboratory and here by analytical experimental tests the effort is made to ascertain to what special agencies the departures are due. Four

main locations furnish the chief facilities for these somewhat extensive experiments, which may be briefly characterized as follows. The domain of the Desert Laboratory has a subtropical arid climate, with one cool moist season, one warm wet season, two intervening dry seasons, the vegetation being chiefly composed of spinose xerophytic shrubs and woody plants, with a large number of the more advanced types of desert plants, which carry an immense water balance, such as the cacti and other succulents. The total rainfall is 12 inches, relative humidity falls as low as 5 per cent. for extended periods and the soil moisture remains below 10 per cent. for weeks, and the altitude is 2,300 feet; maximum temperatures of 112°–114°, minima of about 16° F., with a total exposure below the freezing point of from 12 to 80 hours per annum are encountered.

The xero-montane plantation lies at 5,400 feet on the near-by slopes of the Santa Catalina Mountains at the extreme upper edge of the characteristic desert flora in the oak belt of vegetation with a rainfall of 16 to 18 inches per year, minima a few degrees lower than those of the Desert Laboratory, with such an extension of cold nights as to make temperature a distinct limiting factor; relative humidity is extremely low, soil moisture quite as low as that of the base plantation, and the activity of vegetation of the winter wet season which is such a marked feature of the lower plantation is entirely lacking. The meteoric and other agencies carry a constant stream of seeds from this locality into the region of the laboratory.

The montane plantation lies at an elevation of 8,000 feet in a forest of pine, spruce and aspen, with a climate equivalent to that of northern Michigan, the growing season being about 110 days, the winter being characterized by a heavy snowfall and temperatures as much as 20°–25° below zero Fahrenheit. The spring and autumn are dry, and midsummer has the usual manifestation of heavy thunder-storms, in which the precipitation is

slightly less than the amount in the winter. The yearly total is between 35 and 40 inches. The vegetation is characterized by conifers, grasses and a wide variety of herbaceous and shrubby perennials, very few annuals being found here. The mountain streams carry the seeds of the contiguous elevated slopes and valleys in great profusion to the region of the xero-montane plantations and to the lowlands of the character of those around the Desert Laboratory. These three localities form a connected series in which the behavior of the tested species may be expected to offer phenomena of wide significance and of direct bearing on many phases of geographical distribution and evolutionary advance.

The fourth plantation is at Carmel, California, some 800 miles distant in a straight line from the first three, within a thousand yards of the Pacific Ocean in a forest of Monterey pine, the soil being granitic sand, with organic material or humus in some places, and a heavy cement in others. The climate is characterized by a winter wet season, in which the minima are scarcely below the freezing point and the exposure to such low temperatures is for not more than fifteen or twenty hours per year. A period of heavy continued fogs during two months of the midsummer results in minima of 41° F. in July and August, there being almost no precipitation between March and November. The total precipitation is about 18 inches per annum. The place, therefore, has one rainy season, a dry spring and fall, and a cool midsummer, conditions exceptionally favorable for the survival of species introduced from the localities of the other three plantations of the series. It is obvious that if the data concerning the climatic factors are integrated or summarized and placed in parallel columns a ready means is afforded for detecting the causes which prevent survival or facilitate the development of any form in any locality, and a proper analysis of the same facts may also yield direct suggestions as to the nature of the excitation responsible for any departure on the part of a plant removed from one habitat to another.

The groups of species interchanged among the four different localities include material upon which such analysis may be most readily made. In addition, the introductions are also arranged to simulate certain geographical movements and topographical effects. Species from eastern America and from the lower plantations are taken to the montane and xero-montane plantations to meet conditions similar to those they might encounter in a migration toward alpine or arctic regions. Species from the montane locations and from the eastern states are carried to the desert plantations to have the experience of a southward movement, or that of descending mountain valleys, while all of these localities have furnished forms for establishment in the maritime locality characterized by equable conditions in which species may range widely as to latitude and indefinitely as to longitude. The preliminary exchanges included over a hundred species, mostly biennials and perennials; the survivals amount to less than 80, while perhaps not more than a score of these may be expected to yield results of value or interest.

Our increased insight into the nature of natural groups of organisms has shown the necessity and suggested the means of observing certain distinctions and precautions in this work. Thus it is of the greatest importance that the living material shall be shown to be either simple genotypes or that its phaenotypic nature be apprehended in order that the integration and combination of these forms shall not be mistaken for environic effects. When a lot of plants is taken from one plantation to another, data of the original locality are preserved as the stand of the plant in that place serves as the control. If the plant is multiplied vegetatively in the test, it might reveal a possible complex character of the material in bud-sports, but other divergences might be well ascribed to local effects. On the other hand, if introduced in the form of seeds, the possible complex character of the material would soon become apparent, especially if the generations were followed properly. In the actual management of

the cultures, it is found profitable to re-introduce forms from the original or control lot of various species in order to follow the first stages of their adjustment repeatedly.

The earlier introductions were made in May, 1906, but the establishment of the system was not completed until early in 1909. Some of the species have therefore been observed through the fourth growing season in newly encountered habitats, and as the somatic responses are

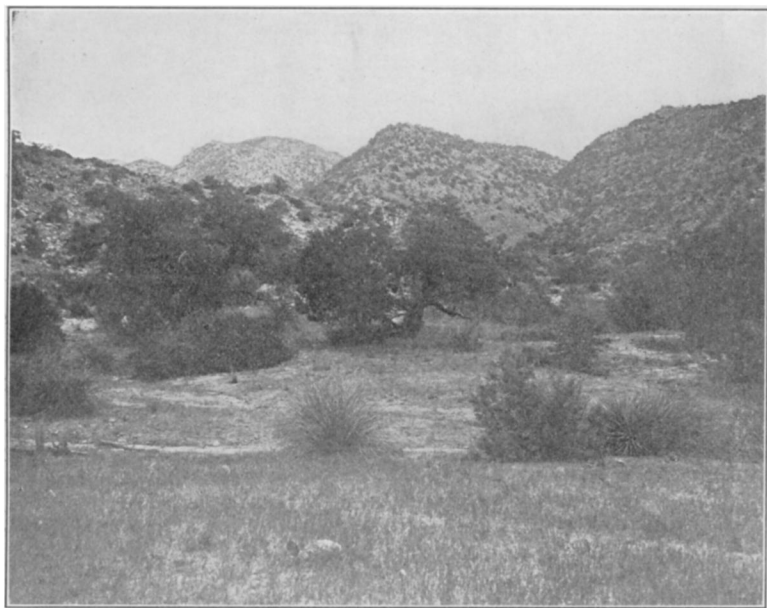


FIG. 3. Xero-montane plantation (5,500 ft.), Santa Catalina Mts., Arizona.

immediate or nearly so it may be assumed with some confidence that the alterations observed are those which are to be tested as to their transmissibility. It may be of interest to note briefly some of the more salient alterations with some attention to their geographical significance, reserving the discussion of structural details for a more suitable occasion.

1. Many species of perennials native to regions in eastern America with a temperate summer or growing

season 160–170 days in length, and a winter with extended exposures below the freezing point, endure the climate of the montane plantation with lower minima, shorter growing seasons and more arid dry seasons, all seasonal changes being much more sudden and pronounced than those encountered in their original habitats. *Trillium*, *Arisæma*, *Roripa*, *Sanguisorba*, *Fragaria* and others offer examples of such survival.

2. Perennials as above survive and thrive in the equable climate of the maritime plantation in which much more equable conditions are found than in the original habitats—*Podophyllum*, *Sanguisorba*, *Arisæma*, *Oenothera*, *Roripa* and *Fragaria*.

It is to be noted that many species of annuals and perennials are supposed to range from the temperate lowlands of New York to similar montane climates farther south in the Rocky Mountain region, and also to the Pacific coastal belt. Critical examination of material representing the supposed inclusion of the species generally reveals differences denoting elementary species or genotypes which might be grouped together in a Linnean treatment. These relationships offer some most interesting probabilities as to derivation and dissemination which may not be touched upon here.

3. Species from the montane plantation survive and show a luxuriant growth in the maritime plantation with various vegetative modifications, of which *Fragaria*, *Oenothera*, *Juglans*, *Scrophularia*, *Senecio* and *Dugldea* offer illustrations.

4. Species from the montane plantation survive and show a development somewhat atypic when carried to the foot of the mountain on which they are indigenous. Examples are *Oenothera*, *Juglans*, *Scrophularia* and *Fragaria*.

5. Species from the arid region about the Desert Laboratory survive and show atypic activity in the equable maritime climate. Illustrations are offered by the *Opuntias*, *Parkinsonia* and *Penstemon*. Species from the

equable maritime location do not survive when taken to any of the other plantations, with the single exception of *Fragaria Californica*, the extremes of temperatures being the evident limiting factor.¹⁹

By the consideration of the responses of plants in the various climates into which they may be introduced in these experiments, it is possible to determine with some accuracy the limiting factors acting for the exclusion of the form in question. The analysis of the responses to changed environment may be briefly given as follows:

Species from locations with well-marked seasons, in which there is a definite contrast between the warm and dry periods or between dry and rainy seasons, show a lessened tendency to sexual reproduction, and a consequent weakened capacity to form fruits and seeds when taken to locations with equable or monotonous conditions. This is a fact well known to the grower of economic plants, the chief examples being offered by bush and tree fruits disseminated to the southward. Fertilization and the preliminary stages of seed formation may ensue as usual, but the absence of the stimulating effect of changing temperatures usually characterizing the close of a season appears to be followed by a lack of development of the fruit. Examples of this are offered by *Arisæma*, *Salomona*, *Sanguisorba*, *Actæa*, *Podophyllum*, *Menispermum*, *Apios* *Fragaria* and *Phytolacca*. Exceptions are offered by *Senecio*, *Oenothera* (some species), *Potentilla*, *Geum* and others.

The transplantation of a species from one type of climatic complex to another generally alters the shoot-habit, or pattern of development of buds. The maritime location is characterized by a profuse development of runners and offsets, and the growth of branches on the lower part of main axis, above or below ground. In some species, the main axis remains in a very rudimentary condition. Excellent illustrations are furnished by *Oenothera*, *Scrophularia*, *Dugaldia* and *Phytolacca*.

¹⁹ See Kuckuck, P., "Ueber die Eingewöhnung von Pflanzen wärmerer Zonen auf Helgoland." *Bot. Ztg.*, Vol. 68: 49-86, April, 1910.

The removal of the higher types of plants from the desert conditions with which they articulate, that is, extreme forms with reduced shoots and swollen stems, is followed by increased development of spines when grown



FIG. 4. Montane plantation (8,000 ft.), Santa Catalina Mts., Arizona.

under equable conditions, or in climates with greater water supply as illustrated by *Opuntia santa rita* and other "spineless" forms.

The removal of plants from localities with well-marked seasons to equable maritime climates is followed by a leaf development which may result in the multiplication of the parts. *Fragaria*. All introductions in which the range of climatic conditions to which the plant was subject was narrowed, were followed by increased vegetative activity, which multiplied underground branches and propagative bodies.

The concurrence of these responses in a single form may be well demonstrated by the results of studies of a genotype near *Scrophularia leporella*, found in the vicinity of the montane plantation, which has survived in the shade at the Desert Laboratory and at the seaside locality. In its native habitat, it shows a strict, scarcely branching shoot with a few fleshy succulent roots, which apparently carry water with a small dissolved content. When this form is taken to the Desert Laboratory, its reproductive season is lengthened from two months to five or six months; although but few seeds are formed, the shoots branch more profusely, and a greater mass of underground members are formed. In the maritime location these features are accentuated and the development of branches goes on to such extent that the shoot gives rise to a number of main branches which can not be supplied with water, and hence soon wilt and die. The underground system now includes dozens of thickened members from one to two centimeters in diameter, which may show a total weight of from 6 to 8 kilograms.

The removals of forms included in the experimental series may be taken as fairly parallel to the distributional movements effected by various agencies without the intervention of man. Some, as a matter of fact, are exact duplicates of occurrences in which these same species participate. The alterations noted are undoubtedly environic effects, and may be attributed chiefly to climatic factors. Two common assumptions as to the behavior of plants are to be noted when species are removed to localities widely separated from the habitat in which they are

found. If they fail to survive or do not flourish in the second location, they are said to have failed to adapt themselves to the new conditions. Into this statement may be read one more in accordance with a physiological consideration of the matter to the effect that the intensities of some of the factors present exceeded the maxima of the plants in question and thus acted as limiting factors to their proper or full development or survival.

The second assumption is to the effect that the alterations displayed by a plant in newly encountered habitats are adaptive and that these changes render the organism displaying them better fitted to meet the conditions. Some reactions are of such a nature as to be of benefit to the plant displaying them, but the worker who assumes that this is true of all changes even in species which thrive and luxuriate in the new habitats will soon find himself widely afield from facts capable of being substantiated by experiments. Thus in the case of the *Scrophularia* noted above, the new maritime habitat includes a congerie of agencies which incite it to form enormous clusters of thickened roots and to exhibit the habit of branching densely. So many branches are formed in fact that the conducting channels at the base of the shoot are incapable of carrying a supply of water adequate to the transpiratory needs of the foliar organs, although the vastly increased balance in the root-system would be sufficient to meet the needs of the plant for days, and consequently the widely spreading shoots of these plants show a large proportion of branches which have about reached maturity and are dying. The behavior of the semi-spineless opuntia (*O. santa rita*) offers illustration of the same sort. Bearing only a few or no spines in its native mountains, the new segments in the cool foggy climate of Carmel are spinose at almost every areole. Here the result is very plainly one of the awakening of a latency, since it seems fairly clear that this plant and all of its relatives show spines as a final stage in the reduction of the shoot system, and that the spineless form is the culmination of a line of progress. The

reappearance of the spines is, therefore, one of regression; in a paper before this society a year ago I was able to present results of experimental parasitism, in which the reactions of autophytic green plants when grown as parasites included a number of phenomena, which were not only not adaptive in any sense, but which might reasonably be considered as distinctly unsuitable. Among these was included the very striking autonomic movements of etiolated segments of the prickly pear (*Opuntia*) when it was led to fasten upon other plants as a parasite.²⁰

Many alterations in plants in the cultures, however, particularly those concerning the reproductive habits, may readily be interpreted as being adjustments of a directly adaptive character. With these are many correlative changes which are simply carried along. It seems fairly certain that the distinction between the primary adjustive alterations and correlative effects will be made clearer in any analyses made of the possibilities of inheritance of somatic changes. In connection with the discussion of the nature of the parasitic adjustments the behavior of a drop of water when resting upon a rough surface was offered as an illustration of the modifications of an organism under environmental influences. The sectors of the drop in direct contact with a hard object which is not wetted will be most markedly and directly altered, in a manner parallel to the reactions in functions most directly affected by environment, while the free sectors or qualities of the drop or of the organism will be altered in various degrees by correlation stresses.

So far as the responses in the cultures at the four plantations are concerned, they appear to the fullest extent at once and in the first generation. Whether any of them may become fixed and transmissible in a long series of generations subjected to the same conditions, like *Daphnia*, remains to be determined. That this might be the most

²⁰ MacDougal and Cannon, "The Conditions of Parasitism in Plants," Pub. No. 29, Carnegie Institution of Washington, 1910, p. 37.

important feature of all experiments of this kind was pointed out three years ago.²¹ Although our attention has been focused chiefly on the possibilities of the transmission of somatic effects by seed reproduction, yet it is to be recalled that the continuation of an alteration by fissions, division or cuttings might come to have great biological significance.



FIG. 5. Maritime plantation near the sea-shore, Carurel, California.

Jennings would consider the *Paramœcia* as free germ cells subject to the direct action of environment, and themselves propagating by simple division if his meaning is properly apprehended. If this is allowable, the same conception may be extended to include cuttings and all fission methods of reproduction in plants, even of the most advanced types. As a general rule, when a portion of the sporophyte of a plant, such as an offset, runner, stolon, tuber, bulb, corm or other detached branch produces a new individual, the mature characters of the parent disappear in the regeneration or sprouting and the

²¹ "Fifty Years of Darwinism," 1909.

ontogenetic procedure of the plantlet will be much like that of a seedling.

The exact observation of the manner in which environic effects may pass the regeneration stage and reappear has not yet been made to any great extent. Doubtless many conditions will be found to affect the process. Bud sports, or vegetative mutations, are, of course, fully transmissible along a series of stages of division by cuttings, and many of them have been found to transmit their divergent characters by seed resulting from close pollination. Mechanically considered, the vegetative reproduction of a plant consists simply of its perpetuation through an unbroken chain of metameres or internodes, each joint arising from a growing point borne terminally or laterally by its predecessor. The projection of induced characters formed by metamere *A* into metamere *B*, therefore, involves the question of germ-plasm as represented by the embryonic mass of the growing points with no opportunity for carrying over structures mechanically as in the *Paramœcium*. The comparative action in heredity when plants are transported to new climates through bulbs and tubers and through seeds is one that has not yet been made, although doubtless horticultural and agricultural literature is rich in the records of facts upon which decisive generalizations might be made.

The genetic character of environic effects remains to be considered. In any species or genotype there is, withal, a limited number of things included within the morphological possibilities. The appearance of any character in an acclimatization culture raises a question at once as to the standing of the new feature. Is it a regressive character, once displayed by the species and now recalled by the very conditions under which it was first induced, or is it to be considered as a character *de novo*, arising simply and directly in response to the external agencies which have been seen to induce it? Thus in the results cited above, our general knowledge of the Cactaceæ leads us to assert with some confidence that the reappearance of a full complement of spines in a prickly

pear from which they had all but disappeared is a regression or return to the condition of the greater majority of the group, a condition which must have been shared by its ancestors at no remote stage in its progressive development.

None of the attempts hitherto made to perfect a theoretical conception which would be useful in interpreting the mechanism of environic responses have had anything more than the most limited usefulness. The stimuli of climatic and many other agencies do not imply the introduction of any strange or new substances into the bodies of the organs affected. These agencies might change the dissociations in such a manner as to modify the relative number of free ions and thus alter the molecular complex of the living matter in a very important manner. The intricate play of enzymatic action might also be altered, and any modification of the relative reaction velocities of the more important processes might result in material and permanent change, especially in those cases in which external agencies interfere directly with the action of the germ-plasm.

The introduction of solutions into ovaries or the exposure of reproductive elements to unusual irradiation may raise the additional liability of disturbed polarity and of modified surface tensions in the cells. It is conceivable that the rearrangement or disturbance of the localizations of substances, especially the mineral salts, might seriously modify the capacities of the bearers of heredity. These direct and material possibilities offer an adequate basis for the organization of experimental research upon the main subject, as well as the means of interpretation of results without recourse to schemes of particulate inheritance or theories as to the constitution of germ-plasm to which may be ascribed usefulness in the discussion of other problems in evolution.

The theoretical consideration of the subject which seeks to assign all cases of inheritance of environic effects to the direct action of the existing agency upon the germ-plasm in itself is one to be regarded with some wariness, as it may lead us into empiric assumptions which may

conceal rather than visualize the actual occurrences. Direct germinal effects are undoubtedly secured in ovarian treatments, and Tower's analytical cultures showed that certain somatic characters induced directly might be secured also by direct excitation of the egg. Such concurrence of reaction may be expected especially with regard to some qualities of simpler organization. Not so readily interpreted are the responses of *Sempervivum*. Alterations in size, number, and structure of floral organs brought about by excitation during ontogeny are surely not coordinate with changes in the germ plasm induced simultaneously. In the case of *Capsella* the transference to an alpine habitat of the plant in the shape of seeds is followed by immediate and direct ontogenetic alterations affecting a multitude of characters. Not until these somatic responses have been repeated, dozens, scores, or perhaps hundreds of times, is an impression made on the germ-plasm that allows it to carry the new characters in the absence of the inducing. These facts suggest to us that the soma is in the closest association with the germ-plasm, has both theoretical and actual qualities different from it, and any changes in these must inevitably be communicated, by the action of hormones or other physiological mechanisms.

A brief paraphrase of the foregoing discussion may be useful in emphasizing some of the more important matters which have been touched upon. It is readily apparent that the assumption of the inheritance of acquired characters, after a long period of tolerance, with but little research activity bearing upon its principal claims, is coming in for a large share of attention from the experimentalist, and there seems a fair prospect that decisive facts may be obtained within a period, very brief in comparison with the century since the principal tenets of the theory were first formulated. Already results are available which have been obtained by cultures of animals from paramoecia to mammals, and of plants from bacteria to the higher seed-plants.

A critical consideration of the available information seems to justify the following generalizations:

External agencies acting upon bacteria, crustaceans, beetles, fungi, and some of the higher types of seed plants have been seen to result in the appearance of new types or genotypes, which have been found to transmit their characters perfectly through so many generations as to indicate practical permanency.

In the greater majority of such cases of changes in heredity, inclusive of Tower's cultures of beetles, Woltereck's experiments with *Daphnia*, Morgan's results with flies, and my own ovarian treatments of seed plants the germ-plasm was exposed to the excitation of unusual climatic factors, irradiation, concentrated nutritive media, or of solutions of sugar or inorganic salts.

The new qualities were seen to be fully displayed, and to appear in a mutational manner in all of these instances, although the new head form acquired by *Daphnia* in Woltereck's experiments did not become fixed and fully heritable until the organism had been kept under the influence of the exciting agency for an extended period, nearly two years. The most recent and one of the most interesting series of results are those which show that the influence of environic factors upon hybridizations by excitation of the germ-plasm may alter materially the results of the unions of identical pairs. This seems to have been first suggested by De Vries and to have been seen by MacDougal in hybrids of mutants of *Oenothera*, while it has been established beyond doubt by the extensive and conclusive results of Tower in crossing beetles under various conditions that environic agencies may exert a very marked effect upon the dominance of paired characters and the general composition of hybrid progenies. A different phase of the matter is represented by the experiments of Kammerer, in which, characters constituting temporary sexual dimorphism mendelize when paired. Aberrants, sports or mutants have been seen to arise and perpetuate themselves under unusual culture conditions in yeasts and bacteria, their survival being dependent upon pedigreed cultures in some cases; and the successive generations were those resulting from fissions, although in some cases spores were interposed.

Many of the purely accommodative adjustments displayed by these organisms and by *Paramœcia* as well as the extremes of variability induced by external agencies and continued by selection, do not become fixed and are not transmissible even in a series of generations by fission. The recent work of Pringsheim, however, shows that some alterations in the way of accommodations or functional responses of yeasts and bacteria to unusual temperatures, culture media, and toxic substances become fixed and transmissible both by fission and through spores. It is not clear, however, that the differential action of the exciting agent upon soma and germ can be made out, and perhaps nothing more definite might be said than that both are directly and simultaneously exposed and exhibit coincident reaction.

When we pass to a consideration of the results of Zederbauer and Klebs, however, the evidence becomes much more decisive. A *Capsella* was found growing at an elevation of 2,000 to 2,400 meters in Asia Minor which had hairy stems, 2-4 cm. long xerophytic leaves, and reddish flowers. This plant had been evidently introduced from the lowlands by man along a route that has been in use for more than 2,000 years. The *Capsella* of the lower plains forms a stem 30-40 cm. high, has whitish flowers and broad leaves; when its seeds are taken to elevations with climates comparable to the above, individuals are developed duplicating those of the highlands, so that the characteristic features of this alpine form are clearly direct somatic reactions; and that they have become fixed and fully transmissible is demonstrated by the fact that in a series of generations grown at lower levels the stem characters, as well as those of the reproductive branches and floral organs, retained their alpine acquired characters, although the leaves, as might be expected, returned to a mesophytic form with broad laminae.

The results obtained by Klebs include divergences of stem habit, number and structure of floral organs in *Sempervivum* which are not capable of being interpreted as functional or adaptive responses to the agencies which called them out and were found to be fully transmissible

by seeds, in which case it is fairly clear that somatically produced characters have been impressed upon the germ-plasm and carried by it to succeeding generations. The structural and functional features displayed by *Sempervivum* in these laboratory experiments are not adaptive in any sense in contrast with those of *Capsella*, which are direct responses.

The actual transplantation of organisms from one locality to another, as a method of experimentation, promises the results of highest value and widest significance, especially when taken in connection with analytical laboratory cultures. This method of approach is one which may yield evidence of the greatest value upon the influence of isolation and other geographical factors, but is also one which allows the repetitive or mnemonic effects to be evaluated. When supplemented by laboratory analyses and cultures to determine the nature of alterations induced, such methods promise results of the greatest value. A series of plantations including locations from mountain tops to the seashore has been established in connection with the Desert Laboratory in accordance with this idea, and in addition to the interchange of species from the various localities a number of introductions have been made from eastern America. Negative or positive results of sufficient inclusiveness to permit analyses as to the nature of the exciting agency and the permanence of the response are yet available.

Some of the characters called out by environic agencies may be retracements, or regressions, as the reappearance of spines in cacti, or they may be awakened latencies or organizations *de novo*. Some of the responses may result in sexual dimorphism, while in others the induced characters may be sex-limited. The alterations induced by external agencies may be cumulative or mutative as to appearance or organization, and they may be permanent upon first appearance, or on the other hand may need generations of repetition before becoming fixed. And lastly the changes may be orthogenetic or heterogenetic as to direction, adaptive and accommodative or correlative, or wholly inutile as to their functional relations.